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# ERIOCAULON DECANGULARE L.; AN ANATOMICAL STUDY.

### THEO. HOLM.

(WITH FIVE FIGURES)

IN a paper entitled "Structure de la racine et disposition des radicelles dans les Centrolepidées, Eriocaulées, Joncées, Mayacées, et Xyridées,"[1] Van Tieghem arrives at the conclusion that these orders possess the same peculiarity in regard to the structure of pericambium as do the Gramineæ and Cyperaceæ, and in this they appear to differ from the other orders of monocotyledons. His conclusions in regard to the Gramineæ and Cyperaceæ, however, are mostly based on the observations of Johannes Klinge, which are recorded in his excellent work, "Vergleichend histologische Untersuchung der Gramineen- und Cyperaceen-Wurzeln."[2] It is the structure of the pericambium, Van Tieghem's *péricycle*, which exhibits such marked variation as to seem characteristic of certain orders, at least in some of the species, and the variation consists in its continuity or interruption by the proto-hadrome vessels. Some very instructive tables are contained in Klinge's paper, in which the position of these vessels has been given in relation to the pericambium of a number of species of Gramineæ and Cyperaceæ. From these tables it is seen that in some species all the proto-hadrome vessels are within the pericambium, in others only half of them or only a few, while in still others they are all in direct contact with the endodermis, having thus broken through the pericambium. Van Tieghem describes the same variation in Eriocaulaceæ, etc. Representatives of no less than seven orders of monocotyledons thus exhibit this peculiar structure.

The continuity of the pericambial stratum is considered

[1] Jour. de Botanique 1 : 305. 1887.

[2] Mém. de l'Acad. Imp. d. sc. d. St. Petersbourg VII. **26** : 12. 1879.

normal, its interruption abnormal. So far, botanists have not ventured to consider these two conditions as anything but specific characters, and if they were really constant they would certainly be of some importance; but my observations have lately shown that they are not to be depended upon as constant in all species. For example, in *Carex hispidula*[3] the pericambium may be interrupted either by all the proto-hadrome vessels or by some of them, while in *C. firma* and *C. supina* this tissue is either continuous or interrupted by the majority of these vessels. These variations were noticed in roots of a single individual, and it is very likely that such irregularities are much more common than is supposed, even in spite of an examination of abundant material. In regard to the Eriocaulaceæ, Van Tieghem describes the root-structure of a few species, and calls special attention to the very regular interruption of the pericambium by all the proto-hadrome vessels in *E. decangulare*, *E. septangulare*, *E. Dregei*, *E. Sellowianum*, and *E. Paraguayense;* while in *E. atratum* and *E. Kunthii* only some of these vessels have broken through the pericambium. Moreover, this author attributes six or eight rays of hadrome to *E. decangulare*, and states that each ray is composed of two vessels, one bordering on endodermis, the other on the central vessel, but separated from it by a layer of conjunctive tissue. Besides Eriocaulon Van Tieghem has described Lachnocaulon,[4] Paepalanthus, and Philodice.

Having observed the irregular disposition of the proto-hadrome in some species of Carex, it seemed well to investigate the matter further, and I have examined the root structure of various other genera, and among them Eriocaulon; and since *E. decangulare* L. exhibits a similar and even more striking variation in its root structure, it was thought worth while to present the results. Furthermore, some notes upon the anatomy of the leaf and stem are appended, for it must be remembered that very little has been published heretofore upon the anatomy of Eriocaulon. As stated above, the root structure has been discussed by Van Tieghem, but only in reference to seven species of the genus; and *E. helichrysoides* is the only one which is treated from a general histological point of view by V. A. Poulsen in his anatomical study of the order.[5] Besides these papers there are some few scattered remarks upon the structure of various organs of the genus in the works of DeBary, Russow, and Schwendener. There is thus only one paper in which a general anatomical treatment of the order has been presented, the work by Poulsen cited above. This author, who has studied fifteen species belonging to nine genera, especially Paepalanthus, all from Brazil, deserves credit for having detected several structural peculiarities; and it is a matter for regret that but one species of the large genus Eriocaulon has been examined.

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[3] On a collection of Carices from Alaska, with remarks upon the affinities of *Carex circinata* and *C. leiocarpa* C. A. Mey. Am. Jour. Sci. IV. 10:279. 1900.

[4] Judging from Van Tieghem's description of the root structure in *Lachnocaulon Michauxii* Kth., it appears that his specimens did not belong to this genus, but to Paepalanthus, and evidently *P. flavidulus* Kth. On the other hand, the structure of our North American *Lachnocaulon Michauxii* resembles that which Van Tieghem has ascribed as peculiar to Paepalanthus.

In the present paper some of the anatomical features of *E. decangulare* will be discussed, and attention will be called to such points as do not harmonize with the conclusions of Poulsen and Van Tieghem in reference to this species and others. The material was collected in sphagnum swamps in the vicinity of Washington, D. C. These swamps are wet during the entire season, so that the plants which were studied were not exposed to any drought during the summer months; furthermore, the plants were almost fully exposed to sunlight. Among the plants associated with Eriocaulon may be mentioned: *Fuirena squarrosa*, *Scleria reticulata*, *Eleocharis tuberculosa*, *Rhynchospora alba*, *R. glomerata*, *R. cephalantha*, *Xyris flexuosa*, *Pogonia ophioglossoides*, *Drosera rotundifolia*, *Utricularia subulata*, *Rhexia Mariana*, and *Asclepias rubra*.

## THE ROOT.

The roots of *E. decangulare* studied were all secondary, being developed from the rhizome. Two kinds may be distinguished: some that are quite thick, white, mostly unbranched, and with few root hairs; and others that are less white, somewhat thinner but decidedly longer, with many lateral rootlets, and amply provided with root hairs. No special arrangement of these two forms was noticed, but the thick ones were perhaps the more abundant. Both forms appeared to have developed in the same year, and I was unable to detect any pronounced difference in their internal structure that might warrant any further distinction than the one observed in their external appearance.

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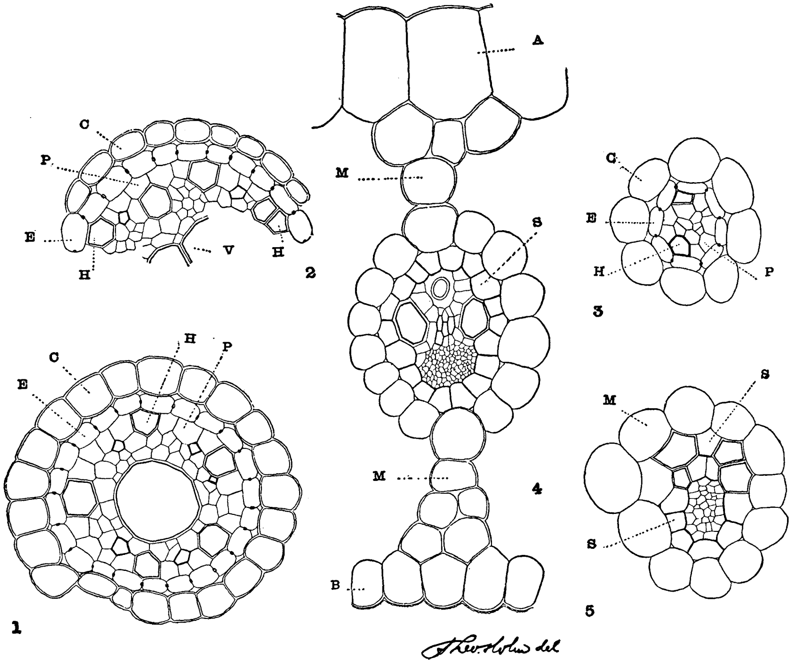
[5] Anatomiske Studier over Eriocaulaceerne. Thesis, Copenhagen. 1888.

The thick white roots show a very weak structure in general, which seems to imply that they are of short duration, and probably do not last beyond one season. The epidermis is very thin walled, and root hairs are present, but rather scarce. The root hairs observed were all single, not in pairs, as Van Tieghem observed in species of Paepalanthus (Lachnocaulon ?). Poulsen did not find any root hairs at all in *E. helichrysoides*, the specimens of which had perhaps not been lifted with sufficient care. Within the epidermis is a hypodermis of a single stratum, the cells of which are of the same size as those of the epidermis, and are also thin walled. The cortical parenchyma is quite broad, but almost totally collapsed radially, excepting the innermost stratum which borders on the endodermis, and which is often somewhat thick walled in contrast with the other portion of the cortex. There are thus several very wide lacunes in the cortex, and these contain horizontally placed diaphragms composed of star-shaped, thick walled cells, which contain chlorophyll. The lateral roots do not immediately break through the epidermis, but traverse the cortex for some distance downwards before they penetrate the hypodermis and epidermis. A similar course of the lateral roots was observed by Poulsen in *Carpocephalus caulescens* Kth.

The endodermis (*fig. 1, E*) is usually thin walled, and the spots of Caspary are plainly visible. However, in some roots the cell walls of the endodermis are slightly thickened, especially in the basal portion of the root. The pericambium (*figs. 1, 2, P*) is very thin walled, and consists of a single layer, which in no case was observed to be continuous, although a very large number



Figs. 1–5. Eriocaulon decangulare L.

Fig. 1. Transverse section of a thick root: *C*, innermost stratum of cortex; *E*, endodermis: *P*, pericambium; *H*, proto-hadrome vessel; the proto-leptome cells are drawn with heavy lines; the drawing shows five proto-hadrome vessels, all bordering on endodermis, and alternating with five groups of leptome; a large vessel occupies the center of the root. × 495.

Fig. 2. Transverse section of a part of a thick root; letters as above; *V*, the two central vessels; one of the proto-hadrome vessels has not broken through the pericambium. × 495.

Fig. 3. Transverse section of a lateral root; letters as above; there are only two proto-hadrome vessels, both of which border on endodermis. × 495.

Fig. 4. Transverse section through a large mestome bundle from the leaf; *A*, epidermis of upper face; *B*, same of lower surface; *M*, the collenchymatic tissue, which surrounds the mestome bundle completely and extends to the epidermis on both faces of the leaf; *S*, the inner sheath, which forms a closed ring around the leptome and hadrome; in the hadrome is a lacune with a ring vessel. × 320.

Fig. 5. Transverse section of a smaller mestome bundle from the leaf; letters as above; the inner sheath (*S*) is interrupted by the vessels. × 495.

of sections were examined. To examine the position of the proto-hadrome in relation to the pericambium, not only were a number of sections taken from roots of various individuals, but also several roots of the same specimen in their entire length from apex to base. The latter method appears to give the most satisfactory results, and is sufficient to demonstrate that neither the position of the proto-hadrome vessels, nor the number of hadromatic rays or of the individual vessels is to be depended upon as a constant character.

A few examples of these structural irregularities are as follows. One of the thick roots possessed at the base eight rays of proto-hadrome, each consisting of a single vessel, five of which had penetrated the pericambium, thus bordering immediately on endodermis. Nearer the apex of the same root the number of rays decreased from eight to seven and to six, five of which had broken through the pericambium, as in the first case. At the apex itself there were only five rays, all of which were bordering on the endodermis; thus the number of interruptions of the pericambium was five in the entire length of this root. In other roots only five rays were found at the base, four of which had broken through the pericambium; and here also there was a similar decrease in number of rays when approaching the apex, where finally all the proto-hadrome vessels bordered on the endodermis. The number of interruptions may vary in the same root, instead of being five, for instance, throughout the entire root; or there may be roots in which all these vessels border on the endodermis, the most frequent condition (*fig. 1*). Van Tieghem ascribes six to eight hadrome rays to this species, each consisting of two vessels, but such regularity in number was not observed in my material. Not only did the number of rays vary, usually decreasing from base to apex, but five was the most common number, each ray consisting of a single proto-hadrome vessel (*fig. 1*, *H*) instead of two. The largest number of rays observed was eight, but this number, as well as seven, was rather rare, while six or four was not uncommon. While the proto-hadrome vessels were observed as being mostly one in each ray, sometimes two, three, or even four together were observed, either in the same radius or side by side. This multiplication of vessels was found in the same root in which the majority of sections showed only a single vessel in each ray.

In considering the pericambium itself another irregularity in respect to the number of cells between each two proto-hadrome vessels was observed. Two may be found in many roots, and is no doubt the commonest number; three cells were found, however, in the same roots, but seldom four or five. The leptome forms groups which are roundish in transverse section, and the proto-leptome is plainly visible. The central portion of the root was constantly found occupied by one or two wide reticulated vessels, mostly surrounded by a thin walled conjunctive tissue.

The thinner secondary roots show much the same structure as described above, but root hairs abound. The innermost stratum of the cortex is sometimes distinctly thick walled, and the endodermis often exhibits a similar thickening of its walls. These roots show the same irregularities in the structure of the pericambium and the hadrome as described above, and there is also a wide central vessel surrounded by a thin walled conjunctive tissue.

The lateral roots exhibit a very simple structure (*fig. 3*). No hypoderm is developed, the cortex bordering immediately on epidermis, and composed of only two or three strata, the innermost of which persists (*fig. 3, C*), while the others sometimes collapse radially. The endodermis (*fig. 3, E*) is very thin walled, the spots being very plainly visible; and the pericambium is interrupted by the two rays of proto-hadrome, which alternate with two minute groups of leptome. No central vessel was observed. The peculiar course of the lateral roots in the cortical parenchyma before they break through the hypoderm and epidermis has been described, and it might be added that root hairs are absent from the enclosed part of these roots, but are developed as soon as the root became free.

The roots of Eriocaulon may well be classified as simply "nutritive," as has been described by Rimbach,[6] since they possess no pronounced power of resistence, and are not contractile or especially adapted for storage.

### THE RHIZOME.

According to Gray's Manual (sixth edition) all our species should be "stemless," but Morong[7] has corrected this and describes for *E. decangulare* a short thick caudex one or two inches in length. This species has a nearly horizontal or ascending rhizome, densely covered by remnants of old leaf bases, with no internodes. The numerous long hairs developed from the epidermis are very characteristic, being pluricellular, the cells in a single row, and the basal cell very short. The cortex is differentiated into two or three subepidermal strata, the cells of which are mostly pentagonal in tranverse section, with distinct but narrow intercellular spaces, and an inner tissue of many layers of nearly roundish thin walled cells containing starch. This portion of the cortex is very open on account of large intercellular spaces, but no lacunes were observed. Within the cortex is an endodermis, the cell walls of which are not thickened and do not show the characteristic spots of Caspary. Nevertheless, the endodermis was readily visible by the peculiar clearness of its cell walls in contrast with the surrounding cortical parenchyma, and by the somewhat irregular shape of the cells. Within the endodermis is a large, solid, fundamental tissue, consisting of somewhat thick walled cells with distinct intercellular spaces, and containing starch. The mestome bundles occur in the cortex and in the fundamental tissue. Those in the latter tissue, being thus within the endodermis, are not arranged in any order, and are mostly bicollateral and perihadromatic, but not always completely so. They are not surrounded by any special sheath, and the vessels are either scalariform and quite narrow or reticulated and wider.

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[6] Beiträge zur Physiologie der Wurzeln. Ber. d. deutsch. Bot. Gesell. **17**: 18, 1899.

[7] Notes on the North American species of Eriocauleæ. Bull. Torr. Bot. Club **18**: 354. 1891.

When the mestome bundles break through the endodermis to the cortical parenchyma, they appear much smaller and are then surrounded by a thin-walled endodermis, showing the same power of resisting concentrated sulfuric acid as does the main endodermis. They are almost regularly arranged in two concentric bands, and are either strictly collateral or more or less bicollateral, in the same manner as those of the fundamental tissue. The general structure of the rhizome, therefore, does not differ from that of other monocotyledonous plants, with the exception of the development of the epidermis into long hairs, which is known in a very few other orders. The mestome bundles of Eriocaulon being collateral or more or less completely perihadromatic do not differ from those of rhizomes of most of the other monocotyledonous orders. Attention may be called, however, to a very peculiar structure which Poulsen discovered in the rhizome and stem of *Actinocephalus polyanthus* Kth. (Eriocaulaceæ), and which may be found in some of the other genera. The mestome bundles exhibit a form very unusual among the phanerogams, in being perileptomatic in the cortex and exohadromatic in the fundamental tissue; in the latter the perihadromatic bundles are surrounded by a tissue which is suggestive of leptome, and around this again is a band of vessels, each mestome bundle consisting thus of a central group of leptome surrounded by two bands of hadrome separated from each other by a band of apparently leptomatic tissue.

## THE SCAPE.

The inflorescence, a capitulum, is borne at the apex of a long, slender, solid and twisted scape, which is distinctly furrowed and consists of only one internode with a single leaf, the long tubular sheath of which surrounds the scape to about its middle. In a transverse section of the free part of the scape, there is shown an epidermis of roundish cells, covered by a thin, smooth cuticle. The size of the cells varies somewhat, and the largest are observable in the furrows, where they cover the green cortex. Stomata and hairs are present and exhibit the same structure as in the leaves, under which they will be described. Underneath the epidermis is either a chlorophyll bearing cortical parenchyma (in the furrows) or a mechanical tissue (in the ridges). The former in our species occurs in nearly rectangular groups in transverse section, separated from one another by the mechanical tissue. There is but one stratum of palisade cells, directly beneath the stomatiferous epidermis; while the other part of the green cortex consists of loosely connected cells of irregular shape and with very wide air spaces. No proper lacunes are developed in the cortex, nor are there any such diaphragms as in the leaves.

The mechanical tissue constitutes quite a prominent portion of the stem section. It is this tissue which forms the eight ridges, and it extends inwards to the mestome bundles, which it surrounds as a closed ring, and also occurs as a few layers on the hadrome side of the mestome bundles. A close examination of this tissue, however, shows that even if it may be designated as "mechanical" throughout, it nevertheless represents two distinct kinds of tissues, collenchymatic and stereomatic, both somewhat modified in our species. The collenchymatic tissue reaches its highest development in the ridges of the scape, just beneath the epidermis. It appears there composed of distinctly thickened cells, but roundish in cross section and with plainly visible intercellular spaces; viewed in longitudinal sections these cells are rectangular and quite long. As mentioned above, this tissue extends inwards between the groups of green cortex to the mestome bundles, and occurs here as a closed ring of two or three strata. I have been unable to discover any distinction between the strata which surround the band of mestome bundles and those which form the ridges. The thickening of the cell walls is of course most pronounced in the ridges, and especially near the epidermis, but if the tissue is followed inwards to the mestome bundles the thickness decreases very gradually, and the shape of the cells remains the same in both longitudinal and transverse sections. The term "collenchymatic," as suggested by Schwendener for this special tissue in

Eriocaulon, seems more suitable than "stereomatic"; moreover, it appears that it attains a still further development in other genera of the order, where it sometimes resembles true collenchyma much more than in our species.

The second form of mechanical tissue in the scape so much resembles stereome in its structure that it may be considered as stereomatic, but not as stereome proper. This tissue is but sparingly developed, and occurs only in one or two strata covering the leptome of the bundles within the collenchymatic ribs, and as a few cells on the hadrome side of these same bundles. The lumen of these stereomatic cells is much narrower than in any portion of the collenchyma; moreover, the cells are longer and the cross walls are almost oblique. In no instance, however, did I observe this stereomatic tissue form a sheath around the mestome bundles; it seems to be restricted to a few strata on either face, separated from one another by the large vessels on the sides of the bundles. The small mestome bundles which are located within the chlorophyll bearing cortex are destitute of such stereomatic support. It would thus appear as if the mestome bundles are merely surrounded by continuous strata of collenchyma which only differs from that in the ridges in being less thick walled; and there is no indication of such structural peculiarities as might lead to a separation of it into two tissues, as a collenchymatic and an endodermal. The cells showed exactly the same shape and size all around the central cylinder, and in no place were the spots of Caspary, or any special arrangement usually noticeable in an endodermis, observed. However, when the sections were placed in concentrated sulfuric acid, a true endodermis became at once plainly visible. The collenchyma was rapidly destroyed, while a continuous ring of a single stratum of cells persisted for some time surrounding the mestome bundles and bordering on the leptome, but separated from it by the few strata of stereomatic tissue. The scape thus possesses an endodermis of the same structure as that observed in the rhizome.

It has been stated already that the mestome bundles occur of two sizes, both constituting a single band, the larger situated in the same radius as the collenchymatic ridges, the smaller in alternation with them within the cortex. The leptome forms quite a large oval or roundish group in both kinds of bundles, all of which are collateral; and the hadrome is composed of very wide reticulated vessels which form a continuous arch in the smaller bundles, sometimes in the shape of a V. In the larger mestome bundles the arch is less complete, and here a small lacune with remains of an annular vessel was observed. This structure of the mestome bundles suggests what is known among other orders of monocotyledons, especially the larger ones. Finally, the pith, which occupies the inner portion of the central cyclinder, is solid, not hollow, but the cell walls are very thin, and no deposits were observed.

The base and apex of the scape show the same arrangement and relative development of the various tissues, but no stomata or hairs were observed on the part enclosed by the tubular leaf sheath. It might be stated, also, that although the mestome bundles were noticed to be strictly collateral in a large number of sections, one instance was found in which a few (three) narrow scalariform vessels were situated outside the leptome, this mestome bundle being thus approximately perihadromatic. It was only in one bundle, however, and very near the inflorescence. The structure of the bundles, therefore, does not seem to be invariably identical throughout the whole length of the stem. It must be remembered, also, that in the rhizome the bicollateral bundles within the endodermis pass gradually over into collateral when they enter the cortical parenchyma, whence they proceed to the leaves, in which they are constantly and strictly collateral.

### THE LEAF.

The proper leaves are linear, nearly flat or with the margins somewhat involute, and have no sheath. They form a dense rosette at the apex of the rhizome, and in their axils the flower bearing scapes develop on very short one leaved shoots, while the terminal bud of the rhizome itself is purely vegetative. In contrast with the proper leaf, the leaf of the floral shoot has a long tubular sheath and a very short blade, and this leaf is by some authors considered as representing the prophyllum of the floral shoot. No other leaf is developed on this shoot, but its true position in relation to the mother axis cannot be ascertained, since the scape becomes twisted during its growth and forces the leaf away from its natural position. Thus the little blade may sometimes turn to the side or to the front, instead of turning its dorsal face towards the main axis, as is the normal position of such a prophyllum. As will be shown later, the structure of this leaf is very different from that of prophylla as a rule, though some analogous cases do exist in other orders, where a similarly developed leaf unquestionably represents a true prophyllum. Attention might be called especially to the clado-prophyllum in the inflorescence of certain Cyperaceæ, as for example, *Scirpus silvaticus*, *S. polyphyllus*, *Cyperus phymatodes*, *C. strigosus*, and many others. So far, there is no very strong objection to considering the leaf of Eriocaulon as a prophyllum, even if its position cannot be determined accurately. There is no very pronounced difference between these two kinds of leaves, but they will be treated separately in order that the view of their general structure may be made as distinct as possible.

The proper leaf, in sections taken from the middle of the blade, shows a large celled epidermis on both surfaces, especially on the upper. There is a thin, but visible cuticle, which shows minute wrinklings on the lower surface, but is smooth on the upper. None of the epidermal cells are arranged so as to form longitudinal rows of bulliform cells, such as are so well known in many genera of Cyperaceæ and Gramineæ, where they especially abound above the keel of the blade or between some of the larger mestome bundles. The cells in Eriocaulon are very large on the upper face, but decrease very gradually in size from the middle towards the margin, the outermost part of which is composed only of the two strata of epidermis corresponding to the two leaf surfaces. Viewed *en face* the radial cell walls are perfectly straight on both surfaces, and the outer cell wall of the dorsal epidermis is somewhat thicker than the others. The inner wall may sometimes show a peculiar bend inwards, the lumen of the cell thus becoming diminished, while at the same time a wide air space is formed beneath the cell. This case was noticed only on the lower face of the blade, and Poulsen found a similar structure, but much further developed, in the leaves of Dimeranthus and Actinocephalus. While hairs are present on both faces of the blade, stomata are restricted to the lower surface. The hairs are small and much shorter than those on the rhizome, consisting of but three cells, the terminal one being the longest. They are closely appressed to the leaf blade and point towards its apex. This form of hair was also observed by Poulsen in *E. helichrysoides*, and its early stage of development is represented in his *pl. 5, figs. 2–4*.

The stomata occur only on the lower surface, outside the mesophyll, and possess very narrow guard cells and subsidiary cells, both of which, especially the former, are raised a little above the surrounding epidermis.

The mesophyll in our species constitutes a very uniform structure throughout, and the leaf in this respect may be considered isolateral. There is no continuous layer of palisade cells on the upper face, but the tissue consists of a single stratum, only some of the cells of which represent true palisade. Most of the other cells are roundish and very loosely connected with one another. On the lower face the cells of the mesophyll show a similar roundish form, but the intercellular spaces are not so wide as on the upper face. A like structure is represented by the mesophyll around the mestome bundles, where it is also composed of a single stratum bordering on the mechanical tissue. The inner portion of the mesophyll is broken down into wide lacunes, one between each two mestome bundles, in which are found numerous diaphragms of star shaped, chlorophyll bearing cells, exhibiting much the same structure as those in the root.

Attention has been called, in connection with the stem, to the difficulty in designating the proper term for the mechanical tissue as it is developed in Eriocaulon; and the same is true in regard to it in the leaf, where there is to be observed collenchyma and another form of tissue which superficially resembles stereome, but which shows such strange occurrence and development that it is not even to be considered as a modification of this tissue. The collenchyma in the leaf is thinner walled than in the stem, and accompanies the mestome bundles mostly as hypodermal groups on both faces. It appears to be more strongly developed on the lower face than on the upper, but each group is composed of only three or four layers of these cells (*fig. 4, M*). Around each mestome bundle is a sheath, which at first glance was considered identical with the parenchyma sheath (*fig. 5, M*), as seen in many genera of other orders. A longitudinal section, however, showed a structure very unlike that of a typical parenchyma sheath. The cells were relatively very long, and I was unable to separate them from the adjoining cells of the collenchyma, inasmuch as they both showed the same rapid dissolution when treated with concentrated sulfuric acid. It is somewhat strange, also, that no trace of this outer sheath was found in the stem, a fact which seems to be in favor of the supposition that it is not identical with a true parenchyma sheath. When such sheaths are developed, they seem to follow the mestome bundles not only in the leaves but also in the stem, at least in those which are in the cortex, but not in the pith.

An examination of one of the large mestome bundles (*fig. 4*) reveals the fact that still another sheath (*S*) occurs within the first. This is distinctly thicker walled than the outer, the cells are very much smaller, and the walls are very bright yellow in contrast with the surrounding collenchyma. In longitudinal section the cells of this inner sheath are quite long, with mostly horizontal cross walls. A study of its occurrence throughout the leaf has assured me that it does not show the same development in all the mestome bundles. In smaller bundles the sheath is a mere arch on the leptome side, while the vessels border immediately on the outer collenchymatic sheath. In the larger mestome bundles there is the same arch on the leptome side, besides one (*fig. 5, S*), or sometimes two or three cells on the hadrome side, between the large vessels. Selecting one of the largest bundles in the leaf, the sheath appears as a closed continuous sheath (*fig. 4, S*) all around the leptome and hadrome. It seems characteristic of this inner sheath to show interruptions in the small mestome bundles, and to become confined in the leptome alone in the smaller of them. I regret that I was unable to decide whether the inner sheath is also developed in the smallest of the mestome bundles, the anastomoses. The tissues are so little differentiated in these that it seemed impossible to decide whether the sheath was present or not; the outer one, however, was plainly visible. So far there would be no valid objection to considering the inner sheath as identical with a mestome sheath,[8] which, in several Gramineæ, exhibits the same kind of interruptions in the various forms of mestome bundles. However, there are two reasons for feeling uncertain about its identity. It is absent in the mestome bundles of the scape, where two or three strata of stereomatic tissue have taken its place within a true endodermis, and in longitudinal section the cells differ in a marked degree from those of a mestome sheath, being very long, with almost horizontal cross walls. Moreover, the thickening of the inner cell wall does not show the same structure as in typical mestome sheaths, where this wall almost constantly exhibits a conspicuous thickening in contrast to the outer wall. When treated with concentrated sulfuric acid, however, the sheath in Eriocaulon showed the same resistance as in the endodermal sheaths in the mestome bundles in the cortex of the rhizome. If the outer sheath represents a parenchyma sheath, one might feel justified in considering the inner as a somewhat modified mestome sheath; but since it does not seem possible to separate the outer sheath from the collenchyma, I can at present suggest no other term for the inner one than simply a protective sheath.

Poulsen attributes two sheaths to the mestome bundles in the leaves of the genera which he examined, and, in accordance with his opinion, the outer sheath would represent true parenchyma, the inner sclerenchyma. He saw, however, that the so-called sclerenchyma does not show the same development in all the bundles, but he makes no allusion to its possible identity with a mestome sheath. The outer sheath is only described as being composed of thin walled cells "stretched longitudinally," which does not seem to indicate that a true parenchyma sheath was observed. The testing of these sheaths with sulfuric acid seems to have been omitted.

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[8] SCHWENDENER, S.: Die Mestomscheiden der Gramineenblätter. Sitzungsber. K. Acad. Berlin 405. 1890.

The mestome bundles of the leaf are almost parallel from the base to near the apex, where they unite and form an apparently single bundle. When viewed superficially the nerves might appear without anastomoses, since the numerous diaphragms filled with chlorophyll make the inner portion of the leaf very indistinct. When the blade is divided into halves the anastomoses may be seen, not at all infrequent, connecting the larger nerves at more or less acute angles. In this way anastomoses become plainly visible even without any further treatment with potassium hydrate, and they are often seen in transverse sections. It seems very surprising that Poulsen did not notice them in any of the fifteen species which he examined, and that he points out the absence of anastomoses as one of the principal characteristics of the order. It may be that they are not developed in any of these fifteen species, but they are certainly very plainly visible in *E. decangulare*, and I have found them also in *E. gnaphalodes* and in *Lachnocaulon Michauxii*.

The structure of the main nerves is very uniform. None of the mestome bundles near the middle of the blade are of any considerable size when compared with others, and it might be said that the leaf has no midrib. It has already been stated that some of the nerves are smaller than others, and that a corresponding variation in regard to the development of the inner sheath is noticeable. However, the hadrome and leptome are common to all the main nerves, but are naturally larger in the thicker mestome bundles than in the thinner. The leptome shows the same structure as in other orders, for example Cyperaceæ, Gramineæ, etc. The hadrome shows several relatively wide vessels (reticulated) besides a lacune, in which there occurs a ring vessel. The arrangement of the vessels is the same as in Gramineæ, etc., and in no instance was there seen the V-shaped hadrome as in the scape. The very smallest of the mestome bundles exhibit both leptome and hadrome in two well differentiated groups, and several narrow vessels are developed in them, bordering immediately on the collenchyma, while the leptome has an arch-shaped support of an inner sheath, constantly incomplete in such small bundles.

The base of the leaf differs but slightly in structure from the middle of the blade. The lacunes are wider, the mesophyll is more irregular, and no palisades were observed; furthermore, the inner sheath of the mestome bundles is somewhat more thickened, but shows otherwise the same kind of interruptions in the small bundles. The epidermis does not seem to have become modified in any respect, and both hairs and stomata occur. The structure of the apex, however, is very different. The epidermis is unchanged, but the mesophyll presents a solid palisade tissue in three layers on the lower face, while the upper one consists of more roundish cells with narrow intercellular spaces; the mestome bundles are fused together into one oval group surrounded by a sheath of thin-walled cells, which evidently corresponds to the outer one, the collenchymatic; and it may be added also that in the apex this sheath is not able to resist sulfuric acid. There is thus a single group of mestome in the apex, and the leptome seems much reduced, while the hadrome occupies a broad space and contains many very wide vessels, especially reticulated. This single mestome bundle is not supported by any hypodermal mechanical tissue or by an inner sheath, as farther down the blade.

## THE PROPHYLLUM.

The prophyllum consists of a very long tubular sheath and a short free blade, in both of which there is much the same structure as in the proper leaf. The tubular portion, however possesses an epidermis of several (three) layers on its morphologically ventral face, and this epidermal tissue is homogeneous in structure, the cells being of the same size and shape throughout. The dorsal epidermis consists of only one stratum, and the cells are about the same size as those of the ventral epidermis. The mesophyll is very open on account of wide lacunes, as in the proper leaf. The mechanical tissue is developed further in the prophyllum than in the other leaves in having larger groups on the dorsal face and in being distinctly thick walled, almost like collenchyma. The mestome bundles are surrounded by this tissue, and also by the inner sheath, which is much less differentiated, however, in this leaf, being totally absent in the smallest bundles. Furthermore, a somewhat weaker development of the hadrome and leptome is to be seen in this portion of the prophyllum. It may be stated that the structure of the collenchyma was plainly followed to several of the cells of the outer sheath; thus there seems little doubt that this sheath actually represents a part of the mechanical tissue itself, instead of being a specially developed parenchyma sheath.

The little blade resembles very much that of the proper leaf, in regard to the epidermis with its hairs and stomata, and the mesophyll with its lacunes; while the collenchyma is separated from the dorsal epidermis by strata of small palisade cells. There is the same distinct thickening of the collenchyma, and very plainly so where it surrounds the nerves; the inner sheath is but very incompletely developed in this portion of the leaf. The mestome bundles are almost orbicular in transverse section, and exhibit the same difference in relative size as described above; and finally anastomoses more frequently occur in the prophyllum from apex to base. Thus the inner sheath is present also in the mestome bundles of the prophyllum, though less completely developed; and the same result was obtained as before when treating the sections with concentrated sulfuric acid, that is, the outer sheath dissolved at once, together with the adjoining cells of the collenchyma, from which it must be considered as inseparable, while the inner sheath showed some resistance wherever it occurred.

## CONCLUSIONS.

In comparing the general structure of *E. decangulare* with that of *E. helichrysoides*, as described by Poulsen, there seem to be certain peculiarities in common which may be characteristic of the order, inasmuch as they have also been observed in some of the other genera. The presence of collenchyma is one of these, although this tissue should not be considered so rare in monocotyledonous orders as Poulsen claims it to be. It is common, for instance, among the Gramineæ, where it is well developed in the nodes; it is also found in the small "pulvini" which occur at the base of the lateral branches in paniculate inflorescences of a number of genera. Moreover, in the Cyperaceæ collenchyma occurs in the basal portion of both rachis and prophyllum in certain species of Cyperus of the subgenera Eucyperus, Diclidium, and Mariscus; besides in such species of Scirpus as possess a large open inflorescence (*S. atrovirens*, *S. polyphyllus*, and others). A still more advanced development of this tissue may be observed in Commelinaceæ, Smilaceæ, and Dioscoreaceæ. It does not seem, therefore, as if this tissue exists only in "a very few monocotyledons." But it seems characteristic of the Eriocaulaceæ examined that the collenchyma, or to be more exact "collenchymatic tissue," occurs as prominent ridges in the stem, that it replaces the stereome in the leaves, and that it surrounds the mestome bundles as a closed sheath. The inner mechanical sheath, noted in the leaves, appears to have several points in common with the mestome sheath of the Gramineæ, yet it does not seem to be identical with this, and perhaps may be characteristic of Eriocaulon. The hairy rhizome constitutes an excellent character of the order, even if a few instances are known in other orders of hairs on underground stems, viz., Corallorhiza, Scheuchzeria, and Mercurialis. Otherwise the structure of Eriocaulon does not differ so very much from that of certain other orders, as Cyperaceæ and Juncaceæ, in which a similar leaf structure is provided with a uniform large celled epidermis (Kyllingia, Cyperus, Fimbristylis, etc.). Also, the structure of the rhizome and roots is not to be separated from that of a number of Gramineæ, Cyperaceæ, etc. The most peculiar structure is exhibited by the scape, not only in the presence of collenchymatic ridges, but also in the mestome bundles surrounded by a common endodermis.

But neither the order nor even the genus can be characterized especially by absence of anastomoses in the leaves, since both occur in Eriocaulon and Lachnocaulon; and the continuity of interruption of the pericambium by the proto-hadrome vessels in the root is not of any importance as a family character, as it is not constant, at least in *E. decangulare*.

It appears, therefore, as if Eriocaulon and its allies possess some characters in common with other monocotyledonous orders, and a few which seem peculiar to themselves. The singular inflorescence which is unique among the monocotyledons, and the floral structure, together with the peculiar habit of these plants, make them very distinct among the other orders, to none of which they make any special approach, not even in respect to their morphological characters.

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